The role of sound production in determining dominance in agonistic interactions between male tree wetas (*Hemideina crassidens*, Orthoptera: Anostostomatidae)

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Abstract

New Zealand tree wetas in the genus *Hemideina* have a resource-defence polygynous mating system, where males compete for ownership of galleries and the females they contain. Large males have previously been shown to have better success in male-male agonistic encounters than small males, and consequently obtain more mating opportunities. However, sound production by stridulation is frequently observed in agonistic interaction between males, but its role in determining the outcome is unknown. Here, we experimentally tested the role of sound production in determining dominance in the tree weta *H. crassidens*. We found that muting a dominant male can result in a change in dominance between rival males, but only if the males are similar in size. Large disparities in the size of combating males overrides any effect of stridulation.

Keywords: agonistic interaction - body size - dominance - *Hemideina* - stridulation - sound production - weta.

Introduction

New Zealand tree wetas (*Hemideina* spp.) are endemic, flightless orthopterans, and are among the heaviest insects in the world (Field 2001b, Koning & Jamieson 2001). Of this genus, *H. crassidens* is one of the most common in the South Island (Field & Rind 1992). They are frequently found in the lowland forests of Westland, Nelson and Marlborough in the South Island, and are also common in Wellington in the North Island (Field & Rind 1992). *Hemideina* wetas exhibit strong sexual dimorphism, with females typically having larger body size than males (Kelly 2005), but males having greatly enlarged heads and mandibles (Field

& Sandlant 1983, Kelly 2005) which they use to fight for possession of galleries. Galleries inhabited by tree wetas are most typically small, tunnel-like chambers in trees (Ordish 1992), but for the alpine wetas, *H. maori*, are cavities between rocks (Jamieson 2002). Regardless of the gallery type, male wetas compete with each other for access to galleries and the females that shelter in them during the day (Field & Sandlant 1983, 2001, Koning & Jamieson 2001, Kelly 2005). This behaviour involves an intruder male attempting to remove a resident male from the gallery, thereby simultaneously taking possession of the gallery and the female(s) within. This type of interaction is stereotypical of a resource defence polygynous mating system (Field & Sandlant 1983, Koning & Jamieson 2001).

It is already been well established that larger males are more successful in gaining control of galleries and mates (Gwynne & Jamieson 1998, Field 2001a, Koning & Jamieson 2001, Jamieson 2002, Leisnham & Jamieson 2004, Kelly 2005), although surprisingly, this does not necessarily equate to higher copulation success (Leisnham & Jamieson 2004). However, one aspect of male-male competition that has received little attention is the role of sound production during agonistic interactions. Sound is produced from a stridulatory apparatus comprised of hundreds of small pegs on the femora which are rubbed against files on abdominal tergite II (Ordish 1992, Field 1993a, 1993b). This appears to be the principal means of communication amongst individuals (Ordish 1992) and occurs in three behavioural contexts; defence, territorial signalling and agonistic interactions between rival males (Ordish 1992, Field 1993a). Of interest here is stridulation in agonistic encounters, which has been observed both during (Field 1993a) and after (Field & Rind 1992) combat between males (Field 2001a). Stridulation in agonistic encounters can be used by both an intruding weta, to signal aggressive intent, and by the resident weta, to signal resistance to the intruder (Field 2001a). As such, it is likely that stridulation is used as form of threat display that is analagous to visual displays of mandible size (Field 1993a). If stridulation is a strong signal of fighting ability, it is possible that preventing a weta from stridulating could result in that weta losing dominance in an agonistic encounter. Here, we tested the role of sound production in determining the establishment of dominance between male wetas by experimentally muting males.

Materials and methods

Nine male and nine female adult wetas were collected from native forest near Hari-Hari (West Coast, South Island). Just nine males were collected as the collection methods are destructive and result in the complete demolition of galleries in the habitat (Field & Sandlant 2001). Male-female pairs were randomly selected and placed into cylindrical plastic containers (20 cm diameter, 25 cm deep) where they were fed with raw carrots and fresh *Pittosporum* sp. leaves, and water was provided in a vial plugged with cotton wool (after Field 1993a). They were kept at 15°C on a reverse light cycle that alternated 12 hours of light with 12 hours of darkness. Because wetas are nocturnally active, experiments were conducted during the night phase of the cycle. Observations were made under red-light and also recorded using infra-red video for later analysis. Before any experiments

were conducted, all carrot, leaves and water vials were removed from the container.

Ten pairs of male combatants were randomly selected, with each of the nine males confronting several different opponents (range 1 – 3). Male-male trials were initiated by introducing a male into a container that already contained a male-female pair. Observations continued until one male had proven dominance over the other by copulating with the female.

The male introduced to initiate a trial was called the intruder, and the male already present was the resident. All males were weighed on an electronic balance to the nearest 0.01 g, and head width, mandible length, and hind leg tibia length were measured with calipers to the nearest 0.1 mm. Relationships between the body attributes were assessed with correlation analysis, and individuals were assigned two trait-based index values. First, all individuals were given a score (S) for each attribute (A), calculated by dividing the value for that individual by the maximum value obtained for that attribute from all the measured wetas ($\max S_A$). This is represented by the formula

$$BI = \left(\sum S_{A_i}\right)^2$$

where S_{Ai} is the score S for body attribute A in individual *i*. Scores for each of the four attributes were averaged and squared to give an overall index of relative body size (BI) for the nine wetas with the formula

$$BI = (\overline{S_{Ai}})^2$$

The dominant male from each trial was muted by applying a low melting point wax (75 % resin and 25 % beeswax) to the stridulatory ridges on the hind legs and abdomen. The ten male-male pairs were then re-matched in a second trial. The males had the same occupational status in the re-match as they did in the original trial.

One possible confounding effect that could influence the outcome of re-matches between males is that individuals may remember the outcome of previous interactions (Field & Rind 1992). Data on the temporal extent of memory in *Hemideina* weta are unavailable, but studies on the field cricket *Gryllus bimaculatus* (Orthoptera: Gryllidae) indicate that memory of agonistic interactions in Orthopterans lasts for less than 24 hours (Adamo & Hoy 1995, Khazraïe & Campan 1997, 1999). To minimise the likelihood that memory played a role in our experiment, muted individuals were left undisturbed for at least four days before being re-matched with the previously subordinate male.

The role of muting in determining changes in dominance was tested with a Chi-squared goodness-of-fit test (Zar 1996). The way in which body size influenced the outcome of this experiment was tested with a binomial general linear model (GLM), in which the difference in relative body size of the two combatants was used to predict the probability of a change in dominance following muting.

Results

Four residents and six intruders established dominance following agonistic interactions, and all body attributes were positively correlated with all others (Table 1). The index of body size BI was a strong predictor of dominance, with larger males more likely to dominate agonistic encounters than small males (linear regression on $\log_{10}$-transformed BI; $F_{1,7} = 7.35$, $P = 0.03$, $r = 0.72$; Figure 1).

The application of wax to a male's stridulatory ridges prevented the

Table 1. Results of Pearson correlation analysis between body attributes of male wetas.

Correlation	*r*	*n*	*P*
head width - mandible length	0.98	9	<0.001
head width - hind tibia length	0.89	9	0.001
head width - mass	0.86	9	0.003
mandible length - hind tibia length	0.91	9	0.001
mandible length - mass	0.82	9	0.006
tibia length - mass	0.80	9	0.009

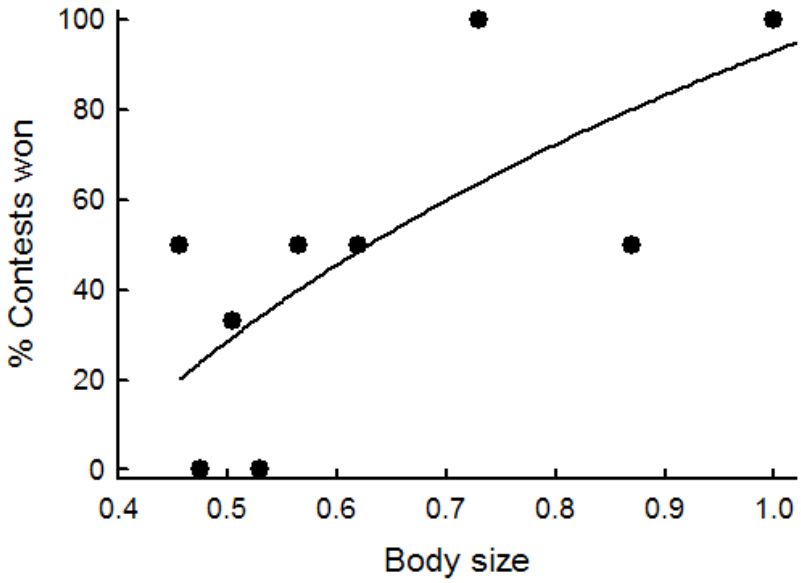

Figure 1. Relationship between body size of male wetas and the probability of them winning agonistic encounters. Body size is an index based on measurements of head width, mandible length, hind tibia length and body mass (see text for details on how the index was constructed).

production of audible sound, but did not prevent that individual from exhibiting stridulatory movements. Dominance was retained by the muted male in eight of the ten re-matches (χ^2_1 = 0.8, n = 10, P > 0.5). However, a binomial GLM (logistic regression) with the absolute value of the difference between body size index values for the two combatants used as a predictor variable indicated that the likelihood of a change in dominance was greater when the two combatants were more similar in size (Figure 2; Deviance = 4.21, Residual deviance = 5.80, df_{effect} = 1, $df_{residual}$ = 8, P = 0.04).

Discussion

Experimentally muting the dominant males did not have a direct effect on their dominance status, indicating that sound production alone played no significant role in the establishment of dominance. However, it is possible that the role of muting in determining dominance was mediated by body size. Although this

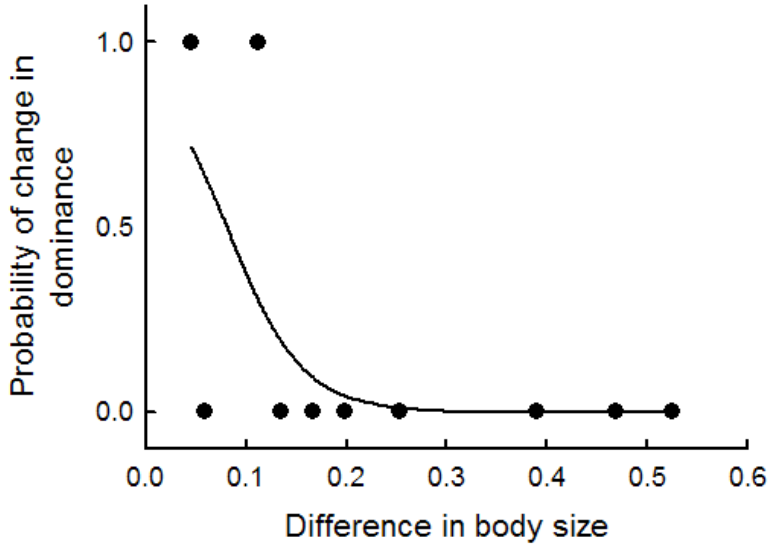

Figure 2. Relationship between the difference in body size of male wetas and the probability that muting a previously dominant male will result in a change in dominance when faced with the same opponent. Body size is an index based on measurements of head width, mandible length, hind tibia length and body mass (see text for details on how the index was constructed).

result was statistically significant, it should be treated with caution because of the low sample size used in this study. Despite this caveat, the results do suggest that males more closely matched in size are more likely to experience changes in dominance, which would indicate that stridulatory behaviour may play a role in agonistic interactions, but that it is not so important that it can override large differences in body size. In other words, an obvious mis-match in size between a large and a small male will always override any effect of sound production.

Unsurprisingly, larger males were more likely to be successful in agonistic interactions than smaller males. Larger males had larger head widths and mandible lengths, which have previously been shown to be strong determinants of success in agonistic encounters (Gwynne & Jamieson 1998, Field 2001a, Koning & Jamieson 2001, Jamieson 2002, Leisnham & Jamieson 2004, Kelly 2005). Mandibles are perhaps the most obvious physical predictor of dominance between male tree wetas, and are used in two ways in agonistic encounters. Initially they are displayed in a threatening manner, opened as wide as possible (Field 1993a). The two combatants then assess each others gape – a combination of head width and mandible length – by contacting each other with their antennae (Field 2001a), and if this does not deter either from engaging in combat, they attempt to outgrip one another (Field 1993a). Presumably, the combination of head width and mandible length provides an opponent with a good indication of an rivals size, and hence the potential winning ability of that rival.

We found no evidence that males gained any advantage from being either the resident or intruder. Field (1993a) observed that *Hemideina ricta* residents won more agonistic encounters than

intruders, a pattern repeated in *H. femorata* (Field & Sandlant 1983). However, these observations were made from agonistic interactions occurring in and around galleries. Presumably, an intruder would have greater difficulty removing a resident from a small, enclosed area like a gallery than they would in forcing a rival away from a female in an open area like our experimental arena. In the latter case, the resident is required to defend a more expansive territory, increasing the difficulty of defence, and thereby eliminating any implied advantage. Future studies should investigate the effect of gallery defence in more detail, as it plays a pivotal role in tree weta behaviour (Field & Sandlant 2001).

Bateman & Toms (1998) investigated male-male interactions in the closely related African king cricket *Libanasidus vittatus* (Orthoptera: Anostostomatidae) in a 'spacious' arena similar to ours. They found that resident males were always victorious and successfully defended their mates. However, they matched males of similar size in their trials to eliminate the effect of body attributes investigated in the present study. Enquist & Leimar's (1983) model of fighting behaviour predicts that large males will defeat small males, and residents will defeat intruders only when there is no size difference. Our study supports the first of these predictions, and that of Bateman & Toms (1998) supports the second.

This study has found no conclusive proof that stridulation by *Hemideina* tree wetas affects dominance between males. Although there is a slight indication that stridulation may play a role in determining the outcome of agonistic encounters between males that are closely matched in body size, further research will be required before this evidence can be considered compelling.

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References

Adamo, S.A., & Hoy, R.R. (1995). Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. *Animal Behaviour* 49: 1491-1501.

Bateman, P.W. (2000). The influence of weapon asymmetry on male-male competition success in a sexually dimorphic insect, the African king cricket *Libanasidus vittatus* (Orthoptera: Anostostomatidae). *Journal of Insect Behavior* 13: 157-163.

Field, L.H. (1993a). Observations on stridulatory, agonistic, and mating behaviour of *Hemideina ricta* (Stemopelmatidae: Orthoptera), the rare Banks Peninsula weta. *New Zealand Entomologist* 16: 68-74.

Field, L.H. (1993b). Structure and evolution of stridulatory mechanisms in New Zealand wetas (Orthoptera: Stenopelmatidae). *International Journal of Insect Morphology and Embryology* 22: 163-183.

Field, L.H. (2001a). Aggression behaviour in New Zealand tree weta. In *The biology of wetas, king crickets and their allies* (ed. L.H. Field), pp. 333-349. CABI Publishing, Oxford.

Field, L.H. (2001b). *The biology of wetas,*

king crickets and their allies. CABI Publishing, Oxford.

Field, L.H., & Rind, F.C. (1992). Stridulatory behaviour in a New Zealand weta, *Hemideina crassidens*. *Journal of Zoology* 228: 371-394.

Field, L.H., & Sandlant, G.R. (1983). Aggression and mating behavior in the Stenopelmatidae (Orthoptera, Ensifera), with reference to New Zealand wetas. In *Orthopteran mating systems: sexual competition in a diverse group of insects* (eds. D.T. Gwynne & G.K. Morris), pp. 120-146. Westview Press, Boulder, Colorado.

Field, L.H., & Sandlant, G.R. (2001). Gallery-related biology of New Zealand tree wetas. In *The biology of wetas, king crickets and their allies* (ed. L.H. Field), pp. 243-258. CABI Publishing, Oxford.

Gwynne, D.T., & Jamieson, I.G. (1998). Sexual selection and sexual dimorphism in a harem-polygynous insect, the alpine weta (*Hemideina maori*, Orthoptera Stenopelmatidae). *Ethology, Ecology and Evolution* 10: 393-402.

Jamieson, I.G. (2002). The relationship between male head size and harem size in the sexually dimorphic mountain stone weta *Hemideina maori*. *Ecological Entomology* 27: 41-48.

Kelly, C.D. (2005). Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. *Behavioral Ecology* 16: 145-152.

Khazraïe, K., & Campan, M. (1997). Stability of dyadic dominance status and recognition of the opponent in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes* 40: 27-34.

Khazraïe, K., & Campan, M. (1999). The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes* 44: 341-348.

Koning, J.W., & Jamieson, I.G. (2001). Variation in size of male weaponry in a harem-defence polygynous insect, the mountain stone weta *Hemideina maori* (Orthoptera: Anostostomatidae). *New Zealand Journal of Zoology* 28: 109-117.

Leisnham, P.T., & Jamieson, I.G. (2004). Relationship between male head size and mating opportunity in the harem-defence, polygynous tree weta *Hemideina maori* (Orthoptera: Anostostomatidae). *New Zealand Journal of Ecology* 28: 49-54.

Ordish, R.G. (1992). Aggregation and communication of the Wellington weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae). *New Zealand Entomologist* 15: 1-8.

Zar, J.H. (1996). *Biostatistical Analysis.* Prentice Hall International, London.